

The Insect Assemblage Visiting the Flowers of the Subtropical Rainforest Pioneer Tree *Alphitonia excelsa* (Fenzl) Reiss. ex Benth. (Rhamnaceae)

GEOFF WILLIAMS^{1,2} AND PAUL ADAM²

¹c/o Department of Entomology, Australian Museum, 6 College Street,
Sydney NSW 2000

²School of Biological Sciences, University of New South Wales, Sydney NSW 2052

Williams, G. and Adam, P. (2001). The insect assemblage visiting the flowers of the subtropical rainforest pioneer tree *Alphitonia excelsa* (Fenzl) Reiss. ex Benth. (Rhamnaceae). *Proceedings of the Linnean Society of New South Wales* **123**, 235-259.

Alphitonia excelsa is a bisexual, protandrous, pioneer rainforest tree. Anthesis and nectar production are diurnal. Populations studied on the Mid-North Coast of New South Wales flower between January and March.

Alphitonia excelsa is dependent upon insects for pollen transfer. Flower-visiting insect assemblages are dominated by Hymenoptera, Coleoptera, and especially Diptera but vary over time, and geographically. Most of the visiting insects were 6 mm or less in size. Approximately 200 genera, from 116 families, were recorded from *A. excelsa* flowers. This fauna comprises taxa that, currently, are known within the region only from *A. excelsa*, and species shared with other mass-flowering rainforest trees. Aculeate wasps were a conspicuous element of the anthophilous insect fauna visiting *A. excelsa* in a littoral rainforest remnant at Harrington. Introduced honey bees, *Apis mellifera*, were active at blossoms at all study sites, but visitation varied over the 3 seasons of study.

Manuscript received 15 August 2001, accepted for publication 21 November 2001.

KEYWORDS: insect assemblages, biodiversity, *Alphitonia excelsa*, pollination, subtropical rainforest, rainforest restoration.

INTRODUCTION

Although Australian rainforests have been subject to an increasing number of ecological studies much recent work has concentrated in the tropics (e.g., Harrington *et al.* 1997, Laurance 1997, Kitching *et al.* 2000), and documentation of the biodiversity of subtropical rainforests is still relatively poor.

We investigated the insect fauna associated with the flowers of the small to medium-sized pioneer tree *Alphitonia excelsa* (Fenzl) Reiss. ex Benth. (Rhamnaceae) (Figs. 1, 2). *Alphitonia excelsa* occurs in the Northern Territory, Western Australia, Queensland, and New South Wales (extending to Mt Dromedary on the far south coast) (Harden 1990). Isolated populations occur inland in the Pilliga Scrub and the Nandewar Ranges (Mt Kaputar National Park) on the New South Wales northern slopes. In New South Wales *A. excelsa* occurs commonly on the margins of littoral rainforest, in floodplain rainforest remnants, submontane subtropical rainforest, wet sclerophyll forest and also occasionally in dry sclerophyll forest. This distribution indicates that the species is a successful coloniser of a broad range of forest subformations and soil types.

The genus *Alphitonia* consists of approximately 20 species distributed in Australia, Malesia and Polynesia. Four of the 6 species occurring in Australia are endemic (Harden 1990). Only the flower-visiting insects of *A. petriei* Braid & C. White have been previously investigated (Irvine and Armstrong 1988). This species occurs in Queensland and uncommonly in northern New South Wales (Harden 1990).

The anthophilous insect visitors, floral structure, floral longevity and flowering phenology of *A. excelsa* in northern New South Wales were studied from 1991 to 1994. Opportunistic observations on flowering phenology continued until 2001. Comparisons were made with the insect assemblages visiting sympatric mass-flowering rainforest species.

Pioneer trees occupy margins and canopy gaps and can occur as senescent emergents above the canopy layer of late-phase regenerating rainforest. Colonising rainforest trees form a distinct subcanopy within wet sclerophyll forests.

Pioneer species generally recruit from a broad spectrum of pollinators and are "usually self-compatible, often autogamous, or reproduce significantly by vegetative means" (Gross 1993, see Baker 1955). In the case of subtropical rainforest pioneers their ability to recruit pollinators from adjacent plant communities, or from the sclerophyllous canopy stratum in wet sclerophyll forests, has been little investigated.

The insect fauna associated with flowering *Alphitonia* will contain species filling a variety of roles, and not all will be pollinators. However, the assemblage will contain pollinators, and within this subset individual species will vary in their efficiency in effecting pollen transfer. We have previously demonstrated that apparently smooth-bodied, and large, insects visiting rainforest flowers (including those of *A. excelsa*) may carry pollen (Williams and Adam 1998), and House (1985, 1989) has documented pollen movement by small-sized insects between tropical dioecious rainforest trees. Consequently, members of the assemblage may, even if incidentally, contribute to pollination but the relative contribution of different species was not studied.

MATERIALS AND METHODS

Investigations were undertaken at three locations; in a littoral rainforest remnant at Harrington (31°52'30"S, 152°41'00"E), and in mixed subtropical rainforest - wet sclerophyll forest at Kenwood Wildlife Refuge (31°44'45"S, 152°31'30"E) and at Lorient Wildlife Refuge (31°45'00"S, 152°32'30"E). The latter two sites were situated on the Lansdowne-Comboyne Escarpment (Williams 1993), approximately 18 km north of Taree on the north coast of New South Wales. This study was part of a larger investigation of the pollination ecology of lowland subtropical rainforest (Williams 1995).

Insect voucher specimens were deposited primarily in the Australian Museum, Sydney, and the Australian National Insect Collection, CSIRO, Canberra.

Flower characteristics

Flower opening, structure, and presence of nectar were determined in the field and by examination of individual florets using a light microscope. Florets were examined under ultra violet light to investigate presence of nectar guides.

Flower Phenology

Observations on flower opening were undertaken at Harrington and Lorient Wildlife Refuge. In addition to *A. excelsa*, all tree species were censused each month, over three seasons (1991-94). At Harrington two marked transects ~ 400-500 m long, separated by 2.5 kms, were traversed. Casual observations of the Harrington *A. excelsa* population continued to 2001. At Lorient Wildlife Refuge a single 600-700 m transect was walked. Observations of *A. excelsa* at the Kenwood site were restricted to the period of sampling during the 1991-92 season only, and only related to the two trees being

sampled. Owing to time constraints we did not record the numbers of trees annually flowering within each population. However, weekly field observations subsequent to and during sampling at Harrington and Kenwood provided finer time scale data on length of flowering for the trees being sampled.

Visitation Periodicity

The number of flowers produced by individual trees is one of many biotic and abiotic factors that can influence recruitment of pollinators (Dafni, Lehrer and Kevan 1997). Variation in the numbers of flowers produced by individual trees was assessed by estimating the ratio of blossoms (buds) to leaf surface (BLS), and by a relative estimate of the percentage of available buds (PAB) on each of the trees sampled. These BLS and PAB ratios are a measure of potential attraction defined by floral resource availability, and can indicate peak periods of foraging activity over the period of flowering by individual trees. The measures are discussed in Williams (1995) and Williams and Adam (1997), however, it needs to be emphasised that the PAB value is a relative measure, because the number of initially available buds diminishes due to fertilisation, floret abortion, herbivore attack, and dislocation by wind and other disturbances generally. Peak BLS values occur at $\geq 50\%$, being a consequence of the physical presentation of flowers and leaves.

Composition of the visiting fauna

The taxonomic composition of diurnal anthophilous faunas was assessed using repeated standardised hand-netting of *A. excelsa* trees (at Harrington and Kenwood Wildlife Refuge), to provide an indication of spatial variation in visiting taxa and their abundance and to assess the daily and seasonal variation in foraging patterns. Opportunistic night spot-lighting of trees in flower was undertaken at Harrington in 1991.

Four trees (2 x 2) were sampled over three years (1991-93) at Harrington and during 1992 at Kenwood Wildlife Refuge. The same trees were sampled each year at the Harrington site. At each site the trees being sampled were more than 20 m apart. Observations of the insects visiting flowers were undertaken on an additional 2 trees at Kenwood (in 1992), and more than 17 trees at Harrington (1991-1993). The insect species observed on these trees did not obviously differ from the trees sampled. Although these additional trees were not sampled, owing to the sample load generated by the broader pollination study (see Williams 1995), occasional insects were individually collected to determine pollen loads (see Williams and Adam 1998).

Day-flying insects visiting inflorescences of *A. excelsa* were sampled using a long hand-held net with a cloth bag that could be quickly detached. Insects could not exit through the cloth wall. Ten inflorescences (= 1 aggregate/composite sample), of similar developmental stage from each of two trees, were sampled by quickly placing the net over each inflorescence and shaking briskly to dislodge all insects. The mouth of the net was closed by rotating the handle to minimise loss of fast-flying insects. This was repeated for the same 2 trees per site, morning and afternoon (i.e. 4 aggregate samples, or 40 subsamples per sampling day) during the 1992 and 1993 seasons, and morning sampling only for the 1991 flowering season. This sampling was carried out approximately once a week, over the entire period of flowering, so that insect diversity and abundance can be related to changes in recruitment cues and potential floral resources (using BLS and PAB values).

Most samples were collected during humid and hot ($> 28^\circ$ Celsius) days, such weather conditions being the seasonal norm at the study sites. Sampling was avoided during cooler periods, during and shortly after rain, and during overcast periods; which are conditions that reduce insect activity and abundance, or reduce floral cues (e.g., by diluting nectar and scent plumes). Consequently, there was occasional variation in sampling time between days.

Following the collection of each aggregate sample the net bag was detached, placed within a plastic container and sprayed with commercial pyrethroid insecticide and sealed for 10-20 minutes. Contents were then emptied into labelled petri dishes for later sorting, measurement and identification.

Insects were assigned to arbitrary size classes, and the number of insects (abundance), and estimated number of 'taxa', as recognisable taxonomic units or morphospecies per insect order or suborder, were recorded for each aggregate sample.

The behaviour of individual species on inflorescences was observed, but no attempt was made to characterise the efficiency of individual taxa as pollinators.

Comparison of fauna with that of other flowering rainforest trees

To gauge whether mass-flowering rainforest trees recruit insects from a shared local (site-specific) assemblage, anthophilous insects collected from *A. excelsa* at Harrington were compared with diurnal insects visiting *Acmena smithii* (Poiret) Merr. and Perry (Myrtaceae), *Euroschinus falcata* J.D. Hook (Anacardiaceae), *Scolopia braunii* (Klotzsch) Sleumer (Flacourtiaceae), *Guioa semiglauca* (F. Muell.) Radlk. and *Alectryon coriaceus* (Benth.) Radlk. (Sapindaceae) at the same site. These are mass-flowering rainforest species that produce numerous open and actinomorphic flowers of a generally similar size and colour to *A. excelsa*. *Acmena smithii*, *E. falcata*, *S. braunii*, *G. semiglauca* and *A. coriaceus* flower earlier in the year than *A. excelsa*, but individual species may not flower each season (Williams 1995). The sampling methodology was the same as that for *A. excelsa*, however, the reduction in flowering episodes reduced the sample base for these species.

RESULTS

Flower characteristics

The small white flowers of *A. excelsa* (Figs. 1, 2) are massed in terminal or axillary cymes and conform to the general entomophilous floral syndrome (Williams and Adam 1994). They are not obscured by foliage. The flowers are protandrous, strongly scented, with an odour reminiscent of urine, and do not possess nectar guides. Sepals 5; petals 4 or 5, rarely 6, reduced and spoon-shaped (spatulate). Stamens antepetalous, 4-5 in number, rarely 6. Style 2-, sometimes 3-lobed, developing after anther dehiscence. There are no obvious nectariferous basal glands, but the receptacle is 'fleshy'. Ovaries are green, petals and filaments white, the filaments being slightly translucent. The sepals and receptacle are greenish-white. Petals and stamens are erect by the time the anthers dehisce, and recurved and held laterally as the ovary develops. Pollen is cream to greenish in colour, translucent, and slightly sticky. At flower opening, and when anthers dehisce, the stamens are encapsulated by the petals (which at anthesis are not fully spatulate in shape). When the petals surrounding the dehiscent anthers are depressed (for example, by a visiting insect) the sticky pollen grains are exuded, in an elongated mass, clear of the encapsulating petals onto flower visitors. Following anther dehiscence, the stamens are carried 'free' or away from the developing ovaries as the encapsulating petals gradually recurve.

Nectar is produced at full flower opening, which is diurnal and occurs between 1030-1300 hours EST. Nectar production ceases upon apparent pollination/fertilisation. Stigmatic lobes become brown following pollination. Mean flower longevity 7 (range 5-9) days (number of flowers sampled = 10).

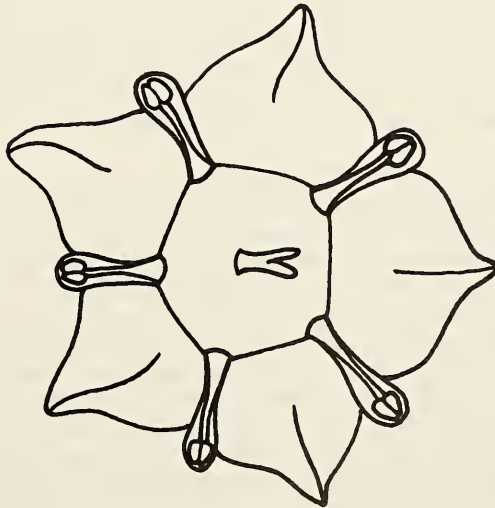
Flowering phenology

Flowering at all sites was restricted to January - March with peak flowering (highest BLS/PAB levels in sampled trees) in February, approximately 2-4 weeks after onset of flowering. However, even at the coarse monthly census scale, records indicate spatial, and suggest interseasonal, variation in flowering (Williams 1995).

Figure 1. *Polistes* wasp on *Alphitonia excelsa* flowers.



Figure 2. *Alphitonia excelsa* floret, c. 4.5 mm diameter.



The individual *A. excelsa* trees sampled at Harrington flowered for approximately 7-8 weeks in 1991, and 6 weeks in 1992 and 1993. Populations at Harrington flowered every year of observation (1991-2001). Length of flowering by the Kenwood population (in 1992) was approximately 6 weeks. However, during three seasons (1991-94) of observation at Lorien Wildlife Refuge *A. excelsa* flowered only in the 1991-92 season, for approximately 6 weeks (Williams 1995). Observations during 1991-94 coincided with a period of drought (Williams 1995) and flowering episodes at Lorien during this period may have been affected by water stress.

Visitation Periodicity

Differences in the number of individuals and taxa recorded in Tables 1-5 suggest temporal variation in insect recruitment, however, this may reflect change in the size and composition of the available pool of insects. The data also indicate variation in numbers of insects and numbers of species visiting individual trees. However, we do not know whether these results represent patterns of daily foraging behaviour by individual taxa, fluctuation in the pool of available pollinators, differential response to recruitment cues entrained by variation in the availability of resources, or environmental influences.

At Harrington in 1991 more individual insects were captured on Tree 2 than Tree 1 during peak phase flowering. Numbers of individuals peaked on the 25th January at both trees, approximately 3 weeks after onset of flowering. Coleoptera comprised a greater proportion of individuals on Tree 1, than Tree 2, while Diptera and Hymenoptera comprised a greater proportion of insects visiting Tree 2 (Table 1). Species at Tree 1 comprised a higher proportion of Coleoptera, and although richness peaked approximately 3 weeks after onset of flowering levels were spread more evenly than Tree 2 throughout the period of flowering (Table 1). The greatest number of species at Tree 2 occurred approximately 2-4 weeks after flowering onset, and comprised mainly Hymenoptera and Diptera (Table 1).

Visitation patterns at Harrington in 1992 varied between trees and between morning and afternoon samples (Table 1). Numbers of individuals and species were generally greatest at mid-phase flowering, approximately 2-3 weeks after onset of flowering. On Tree 1 Diptera dominated early phase flowering but steadily reduced in proportion throughout the season. There were no parallel trends on Tree 2. Greatest number of individual Hymenoptera occurred on both trees during peak availability of floral resources, approximately 2-3 weeks after flowering onset. There were no clear trends in numbers of species within individual insect orders, however, there was an overall peak in number of species approximately 2-3 weeks after flowering onset.

Visitation in the final 1993 sampling season at Harrington was characterised by early phase Hymenoptera and Diptera peaks. There continued to be variation between trees in numbers of individuals and species (Table 1).

At the Kenwood site Hymenoptera and Coleoptera occurred in fewer numbers than Diptera, but there was no obvious pattern (Table 2).

Total numbers of individuals and species (as means) were plotted against increments in blossom:leaf surface (BLS) and percentage of available bud (PAB) values. Numbers of individuals and species, measured against BLS ratios peaked in mid phase flowering (Fig. 3). However, measured against PAB values, there was a distinct late phase peak, but with no clear trend over the period of flowering (Fig. 4). The late phase peak may be interpreted as a concentration of insects on diminishing floral resources at the conclusion of flowering, and lack of alternative mass-flowering trees late in the season (Williams 1995), or changes in the regional pool of available insects.

Table 1. Differences between insects collected in morning and afternoon samples, Harrington, 1991-1993 (1991 sampled only in morning, 'indiv.' = number of individuals, 'spp.' = number of species; 'm' = morning, 'a' = afternoon samples, 'Fin' = finished flowering).

1991

Tree 1	3 Jan		11 Jan		19 Jan		25 Jan		1 Feb		9 Feb		14 Feb		22 Feb	
	indiv.	spp.	indiv.	spp.	indiv.	spp.	indiv.	spp.	indiv.	spp.	indiv.	spp.	indiv.	spp.	indiv.	spp.
Hymenoptera 'm'	0	0	6	6	9	8	13	1	10	8	10	8	11	7	4	4
Hymenoptera 'a'	0	0	1	1	7	6	15	11	9	8	9	8	4	4	2	2
Diptera 'm'																
Diptera 'a'																
Coleoptera 'm'	2	2	6	6	8	8	15	15	4	4	7	7	4	4	6	6
Coleoptera 'a'																
misc. taxa 'm'	0	0	0	0	0	0	1	1	2	2	1	1	1	1	2	2
misc. taxa 'a'																
BLS:PAB values	>30:<1		40:<30		40:50		30:<40		30:>80		30:>90		<30:100		<10:Fin	
Tree 2																
Hymenoptera 'm'	4	4	3	2	45	14	49	15	29	16	16	3	7	1		
Hymenoptera 'a'																
Diptera 'm'	3	3	2	2	23	11	74	14	18	11	17	10	0	0		
Diptera 'a'																
Coleoptera 'm'	8	3	4	2	1	1	1	1	9	3	2	1	1	1		
Coleoptera 'a'																
misc. taxa 'm'	1	1	4	2	2	2	0	0	0	0	1	1	1	1		
misc. taxa 'a'																
BLS:PAB values	>30:5		40:-		60:>50		50:>50		<40:>70		20:100		<10:Fin			

Table 1 continued

1992

	3 Feb		12 Feb		20 Feb		28 Feb		6 Mar		12 Mar	
Tree 1	indiv.	spp.	indiv.	spp.	indiv.spp.	indiv.	spp.	indiv.	spp.	indiv.	spp.	
Hymenoptera 'm'	4	4	15	9	68	14	28	7	9	7	1	1
Hymenoptera 'a'	15	9	24	4	99	20	26	15	19	10	0	0
Diptera 'm'	80	14	62	16	43	20	43	20	21	17	3	3
Diptera 'a'	21	13	31	15	24	15	50	22	15	9	8	7
Coleoptera 'm'	8	3	16	11	18	5	23	7	10	6	12	5
Coleoptera 'a'	7	3	6	3	15	6	22	13	6	2	6	6
misc. taxa 'm'	2	2	4	3	3	3	4	4	4	4	4	4
misc. taxa 'a'	0	0	2	2	1	1	5	5	2	2	1	1
BLS:PAB values	0:<10		50:30		>50:>60		50:10		30:>99		<10:Fin	

Tree 2

Hymenoptera 'm'	4	3	23	9	106	30	37	13	21	8	3	2
Hymenoptera 'a'	4	4	26	9	30	11	39	13	27	12	4	4
Diptera 'm'	55	24	124	27	60	27	70	30	27	16	65	5
Diptera 'a'	31	15	35	11	27	10	109	26	16	15	10	9
Coleoptera 'm'	7	5	15	8	31	8	21	5	27	5	12	3
Coleoptera 'a'	5	3	10	7	13	6	16	6	13	2	24	6
misc. taxa 'm'	2	2	9	5	8	5	3	2	6	4	3	3
misc. taxa 'a'	1	1	2	2	0	0	8	6	3	2	3	2
BLS:PAB values	0:<10		40:30		>50:>50		>60:>95		40:>95		<20:Fin	

1993

	28 Jan		4 Feb		11 Feb		1 Mar	
Tree 1	indiv.	spp.	indiv.	spp.	indiv.spp.	indiv.	spp.	
Hymenoptera 'm'	63	17	31	9	35	10	32	7
Hymenoptera 'a'	10	9	22	9	22	11	7	7
Diptera 'm'	89	21	27	12	20	13	11	8
Diptera 'a'	10	8	20	9	9	8	13	11
Coleoptera 'm'	19	10	29	4	8	6	4	4
Coleoptera 'a'	1	1	8	1	20	2	5	3
misc. taxa 'm'	0	0	0	0	4	4	7	7
misc. taxa 'a'	1	1	0	0	0	0	3	1
BLS:PAB values	40:20		-		40:30		<10:80	

Tree 2

Hymenoptera 'm'	13	5	7	5	17	8	11	5
Hymenoptera 'a'	17	10	14	7	10	6	10	8
Diptera 'm'	32	14	2	2	10	7	11	8
Diptera 'a'	87	16	1	1	1	1	14	11
Coleoptera 'm'	3	3	2	2	7	4	5	2
Coleoptera 'a'	6	4	2	1	3	1	3	3
misc. taxa 'm'	2	2	0	0	2	2	3	2
misc. taxa 'a'	4	2	0	0	0	0	3	3
BLS:PAB values	<20:<10		<20:<20		-		<10:80	

Table 2. Differences between insects collected in morning and afternoon samples, Kenwood Wildlife Refuge, 1992 ('indiv.' = number of individuals, 'spp.' = number of species; 'm' = morning, 'a' = afternoon samples).

Tree 1	6 Feb		13 Feb		22 Feb		29 Feb	
	indiv.	spp.	indiv.	spp.	indiv.	spp.	indiv.	spp.
Hymenoptera 'm'	23	14	15	14	14	12	32	19
Hymenoptera 'a'	23	14	13	11	24	11	16	5
Diptera 'm'	139	23	180	28	114	24	515	44
Diptera 'a'	43	15	62	17	104	21	131	21
Coleoptera 'm'	4	4	6	5	5	4	13	11
Coleoptera 'a'	7	4	8	7	3	3	10	6
misc. taxa 'm'	8	5	9	7	8	3	7	6
misc. taxa 'a'	2	2	5	4	4	4	8	7
BLS:PAB values	<30:<5		<30:<20		40:50		30:>90	
Tree 2								
Hymenoptera 'm'	56	30	22	19	35	18	13	11
Hymenoptera 'a'	110	50	304	51	49	26	39	18
Diptera 'm'	127	22	139	32	97	20	85	27
Diptera 'a'	289	45	370	54	109	22	165	35
Coleoptera 'm'	23	16	38	14	14	8	30	11
Coleoptera 'a'	24	19	29	12	4	4	20	11
misc. taxa 'm'	6	6	9	7	11	7	9	6
misc. taxa 'a'	12	6	13	5	5	5	10	7
BLS:PAB values	40:20		40:>60		30:>90		30:>90	

Composition of the visiting fauna

No vertebrates, including nocturnal mammals, were observed visiting *A. excelsa* flowers during this study. Although several species of passerine birds (e.g., *Zosterops lateralis*, *Meliphaga lewinii*) foraged for insects amongst foliage and seed clusters, no birds visited flowers. Pollination is achieved principally or solely by insects.

Day-time flower visitors were largely Diptera, Hymenoptera and Coleoptera which collectively constituted more than 96 percent of the fauna sampled at Harrington and Kenwood Wildlife Refuge (Table 3). Miscellaneous taxa were principally Hemiptera but also included Blattodea, Thysanoptera, Lepidoptera, Psocoptera, Orthoptera and Collembola. There were considerable differences in the proportion of individual insects and insect orders collected between the two sites, and between seasons at the Harrington site. Flower visitors at Harrington were dominated by Hymenoptera (~37%: range 27.1 - 46.8) and Diptera (~49%: range 27.8 - 52.6) (Table 3). Diptera were dominant at Kenwood and averaged approximately 72% of the diurnal anthophilous fauna. These values compare with those reported by Ireland and Griffin (1984) who record that, on average, approximately 30% of individual insects, visiting *Eucalyptus muelleriana* A. Howitt (Myrtaceae) in East Gippsland, Victoria, were Diptera and approximately 37% were Hymenoptera. In contrast, Hingston and Potts (1998) found, although there was variation between their study sites, that approximately 68% of all individuals (including introduced *Apis mellifera*) visiting flowers of *Eucalyptus globulus* Labill. in eastern Tasmania were Hymenoptera and only 4% were Diptera.

Figure 3. Mean number of individuals and taxa in 10% increments of BLS.

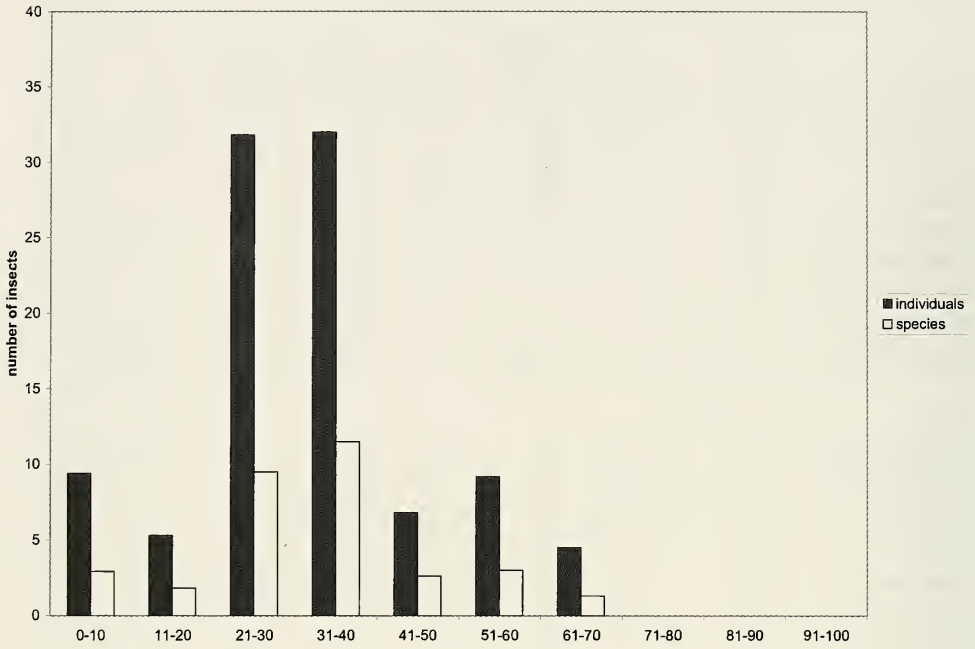


Figure 4. Mean number of individuals and taxa in 10% increments of PAB.

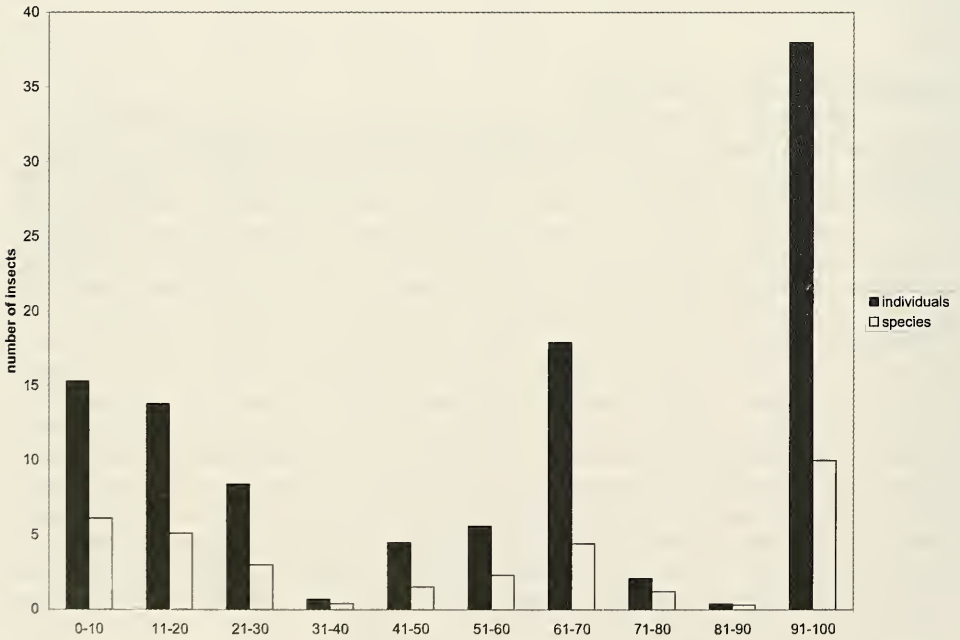


Table 3. Number of individual insects collected in netted aggregate inflorescence samples (number of days sampled and number of aggregate samples taken each day given in parentheses with total insects collected; Harrington 1991 sampled only in morning, Harrington 1992-3 and Kenwood 1992 sampled morning and afternoon).

	Harr. 1991	% of total	Harr. 1992	% of total	Harr. 1993	% of total	Kenwood 1992	% of total
Tree 1								
tot. insects	169 (8:1)		886 (6:2)		530 (4:2)		1557 (4:2)	
tot. Coleoptera	52	30.8	149	16.8	94	17.8	56	3.6
tot. Hymenoptera	63	37.3	304	34.3	222	41.9	160	10.3
tot. Diptera	47	27.8	401	45.3	199	37.5	1290	82.9
tot. misc. taxa	7	4	32	3.6	15	2.8	51	3.3
Tree 2								
tot. insects	327 (7:1)		1195 (6:2)		302 (4:2)		2266 (4:2)	
tot. Coleoptera	26	8	194	16.2	31	10.3	182	8
tot. Hymenoptera	153	46.8	324	27.1	99	32.8	628	27.7
tot. Diptera	137	42	629	52.6	158	52.3	1381	60.9
tot. misc. taxa	11	3.5	48	4	14	4.6	75	3.3
Total insects	496		2081		832		3823	

Although Kenwood was sampled during one season the number of individuals collected was much greater than that collected during individual seasons at Harrington (Table 3). Spot-lighting at Harrington indicated that small Diptera (e.g., Nematocera) and Coleoptera (e.g., Anthicidae, Scirtidae, Scarabaeidae - Melolonthinae) were active on inflorescences at night.

Overall, the majority of insects occurred within the <3 mm - 6 mm size range (Tables 4, 5), however, there was a substantially larger proportion of small-sized fauna at the Kenwood site (97.4 %). The proportion of small-sized insects collected in samples at Harrington did not vary substantially between years (1991: 83.2 %, 1992: 80.9 %, 1993: 86.3 %).

Insect families and genera identified from *A. excelsa* flowers at Harrington and Kenwood Wildlife Refuge are listed in Appendix 1. A list of species is given in Williams (1995). All taxa could be determined to family level, and most could be determined to genus. A small proportion of the collected insects (<5%) could not be determined to genus, and these are cited as numbers of species present in Appendix 1. All taxa are able to contact anthers and stigma.

Data in Appendix 1 indicate seasonal and spatial variation in the insect fauna. Although numbers of individuals collected in netted samples from Kenwood Wildlife Refuge were substantially greater than those collected in any of the three seasons at Harrington, *A. excelsa* flowers at the later site were visited by a much larger number of taxa.

Collectively 116 families, comprising approximately 200 genera (the determination of some genera cited in Appendix 1 is uncertain), were recorded from Harrington and Kenwood Wildlife Refuge. One hundred and four families were collected from inflorescences sampled at Harrington over the total study period (Appendix 1). Seventy-one families were recorded from the Kenwood site, sampled over a single season (1991-92). Seventy-eight families were recorded from the Harrington site in the same season.

Coleoptera comprised 23 percent of families, Diptera comprised 26 percent of families, and Hymenoptera comprised 30 percent of families collected at Harrington. Comparative values from Kenwood Wildlife Refuge were Coleoptera 31, Diptera 28 and Hymenoptera 25 percent of families respectively.

At Harrington there was a high number of aculeate wasp taxa (Williams and Adam 1995) (Appendix 1) in the families Pompilidae, Scoliidae, Sphecidae, Vespidae and Tiphiidae. Only single species of *Rhagigaster* (Tiphiidae), *Scolia* (Scoliidae), *Sphex*, *Sphodrotes* and *Tachysphex* (Sphecidae) occurred at Kenwood Wildlife Refuge. The fly fauna at Harrington was particularly rich in Platystomatidae (9 spp.), Stratiomyidae (6 spp.), Sepsidae (6 spp.) and Tachinidae (10 spp.), many species of which were unrecorded from mass-flowering rainforest trees elsewhere in the region (see Williams 1995). Nine butterfly, 5 ant and 7 tachinid genera were collected at Harrington, but none were collected or observed visiting flowers at Kenwood. There was variation in the native bee fauna, but only *Homalictus* (Halictidae) and *Heterapoides* (Colletidae) were shared between Harrington and Kenwood. The native apid *Trigona carbonaria* was only recorded from Kenwood Wildlife Refuge.

The introduced honey bee *Apis mellifera* occurred at both sites. *Apis mellifera* represented approximately 25 percent of total insects collected at Harrington in 1992, but only approximately 2 percent of insects collected in 1991 and 7 percent of insects collected in 1993 at the same site. Of the 375 insects collected in the 9-12 mm size class at Harrington in 1992, 317 were *A. mellifera*. Honey bees represented 2.5 percent of all insects collected at Kenwood in 1992. Data on bee visitation is discussed in more detail in Williams and Adam (1997).

Flower-dependent insect species peculiar to *A. excelsa* at Harrington, and not recorded elsewhere in the region (see Williams 1995, pers. observations), included the specialised rhipiphorid *Macrostagon* sp., the calliphorid *Stomorhina melastoma*, the syrphid *Dideopsis* sp. and a number of aculeate wasps (Williams and Adam 1995). The records for *Dideopsis* sp. and *Stomorhina melastoma* extend their known distribution south from Indonesia, Papua New Guinea and Queensland (Kurahashi 1989, Thompson and Vockeroth 1989). Four buprestid species in the nectivorous genus *Castiarina* (*C. acuminata*, *C. neglecta* - Harrington, *C. producta*, *C. oblita* - Kenwood) were collected from *Alphitonia excelsa* flowers, and represent new adult host plant records for these taxa. *Castiarina acuminata* collected from *Guioa semiglauca* at Harrington (see Appendix 2) also represents a new adult host record.

A number of species collected from *A. excelsa* also visit the flowers of regional non-rainforest plants (G. Williams unpublished data), however, these generally flower no later (and normally earlier) than *A. excelsa*. These include the Coleoptera *Castiarina neglecta* (*Leptospermum* - Myrtaceae), *Torresita cuprifera* (*Leptospermum*, *Melaleuca* - Myrtaceae), *Jacksonia* - Fabaceae, *Ceratopetalum gummiferum* - Cunoniaceae), *Ophidius histrio* (*Baeckea* - Myrtaceae), *Eupoecila australasiae* (*Kunzea*, *Melaleuca* - Myrtaceae), *Polystigma punctatum* (*Melaleuca*), *Glycyphana brunnipes* (*Syncarpia*, *Melaleuca* - Myrtaceae), *Phyllotocus australis* (*Hakea* - Proteaceae, *Actinotus* - Apiaceae, *Leptospermum*) and *Cheiragra ruficollis* (*Leptospermum*). Species from additional higher taxa await identification.

Comparison of fauna with other flowering rainforest trees

Insect species shared between flowering *Alphitonia excelsa*, *Acmena smithii*, *Euroschinus falcata*, *Scolopia braunii*, *Guioa semiglauca* and *Alectryon coriaceus* at Harrington are listed in Appendix 2. More exhaustive sampling is likely to expand this list. A full list of species collected from each of these plants, and other rainforest trees sampled in the region, is given in Williams (1995). Months and years in which *A. smithii*, *A. coriaceus*, *G. semiglauca*, *E. falcata* and *S. braunii* flowered and were sampled are given in Appendix 2. Unlike *A. excelsa* populations, that flowered heavily each year at Harrington, flowering of these species was more variable and occurred, generally, over shorter time spans (Williams 1995).

Table 4. Size distribution of individual insects collected in netted samples ('m' = morning, 'a' = afternoon).

Harrington 1991 (15 daily aggregate samples; no afternoon samples collected)

	<3mm		3-6mm		6-9mm		9-12mm		>12mm	
	m	a	m	a	m	a	m	a	m	a
Hymenoptera										
total insects	114		28		59		13		2	
mean	7.6		1.2		3.9		0.9		0.1	
range	0-28		0-5		0-29		0-7		0-1	
Diptera										
total insects	154		26		3					
mean	10.3		1.7		0.2					
range	0-69		0-10		0-3					
Coleoptera										
total insects	48		27							
mean	3.2		1.8							
range	0-10		0-5							
misc. orders										
total insects	10		4		1		2		1	
mean	0.7		0.3		0.07		0.1		0.1	
range	0-3		0-2		0-1		0-1		0-1	
Total	316		85		63		15		3	
percent	65.6		17.6		13.1		3.1		0.6	

Harrington 1992 (12 daily aggregate samples)

	<3mm		3-6mm		6-9mm		9-12mm		>12mm	
	m	a	m	a	m	a	m	a	m	a
Hymenoptera										
total insects	62	51	15	23	43	59	183	184	16	6
mean	5.2	4.3	1.3	1.9	3.6	4.9	15.3	15.3	1.3	0.5
range	1-15	0-9	0-3	0-5	0-18	0-19	0-70	0-67	0-11	0-2
Diptera										
total insects	465	322	111	45	14	6	1	2	5	
mean	38.8	26.8	9.3	3.8	1.2	0.5	0.1	0.2	0.4	
range	6-116	6-93	0-47	0-14	0-7	0-2	0-1	0-1	0-3	
Coleoptera										
total insects	218	104	34	37	1	1				
mean	18.2	8.7	2.8	3.1	0.1	0.1				
range	5-28	2-22	0-8	0-8	0-1	0-1				
misc. orders										
total insects	27	21	15	8	4		4	1	3	
mean	2.3	1.8	1.3	0.7	0.3		0.3	0.1	0.3	
range	0-5	0-6	0-4	0-2	0-2		0-2	0-1	0-2	
Total (m+a)	1270		247		128		375		30	
percent (m+a)	61.4		19.5		6.2		18.1		1.5	

Table 4 continued

Harrington 1993 (8 daily aggregate samples)

	<3mm		3-6mm		6-9mm		9-12mm		>12mm	
	m	a	m	a	m	a	m	a	m	a
Hymenoptera										
total insects	50	31	73	48	39	15	20	16		
mean	6.3	3.9	9.1	6	4.9	1.9	2.5	2		
range	1-21	1-6	0-19	0-13	0-10	0-6	0-9	0-6		
Diptera										
total insects	159	124	39	26	4	4	1		1	1
mean	20	15.5	4.9	3.3	0.5	0.5	0.1		0.1	0.1
range	1-74	0-76	0-14	0-8	0-1	0-3	0-1		0-1	0-1
Coleoptera										
total insects	63	40	8	6	3	2	1		1	
mean	7.9	5	1	0.8	0.4	0.3	0.1		0.1	
range	0-28	0-20	0-3	0-2	0-2	0-1	0-1		0-1	
misc. orders										
total insects	12	10	4	3	1		1		1	
mean	1.5	1.3	0.5	0.4	0.1		0.1		0.1	
range	0-5	0-4	0-2	0-2	0-1		0-1		0-1	
Total (m+a)	489		207		68		39		4	
percent (m+a)	60.6		25.7		8.4		4.8		0.5	

Kenwood Wildlife Refuge 1992 (8 daily aggregate samples)

	<3mm		3-6mm		6-9mm		9-12mm		>12mm	
	m	a	m	a	m	a	m	a	m	a
Hymenoptera										
total insects	177	352	3	20	1	6	28	47	1	
mean	22.1	44	0.4	2.5	0.2	0.8	3.5	5.9	0.1	
range	11-40	7-134	0-2	0-7	0-1	0-3	0-15	1-7	0-1	
Diptera										
total insects	1340	1173	56	45		1				
mean	167.5	146.6	7	5.6		0.1				
range	82-488		43-409		1-27	0-12		0-1		
Coleoptera										
total insects	92	85	36	23	3	2	2	3		
mean	11.5	10.6	4.5	2.9	0.4	0.3	0.3	0.4		
range	2-28	1-13	0-14	0-7	0-1	0-2	0-2	0-1		
misc. orders										
total insects	46	52	20	8				1		
mean	5.8	6.5	2.5	1				0.1		
range	2-8	2-5	0-6	0-2				0-1		
Total (m+a)	3317		211		13		81		1	
percent (m+a)	91.6		5.8		0.4		2.2		0.03	

Table 5. Size distribution of mean number of species collected in netted samples (total numbers are not given because taxa are shared between individual samples; 'm' = morning, 'a' = afternoon).

Harrington 1991 (15 daily aggregate samples; no afternoon samples collected)

	<3mm		3-6mm		6-9mm		9-12mm		>12mm	
	m	a	m	a	m	a	m	a	m	a
Hymenoptera										
mean	3.7		1.3		0.7		0.7		0.1	
range	0-8		0-3		0-3		0-5		0-1	
Diptera										
mean	4.8		1.1		0.1					
range	0-11		0-4		0-1					
Coleoptera										
mean	1.9		1							
range	0-8		0-3							
misc. orders										
mean	0.6		0.3		0.07		0.1		0.1	
range	0-2		0-2		0-1		0-1		0-1	

Harrington 1992 (12 daily aggregate samples)

	<3mm		3-6mm		6-9mm		9-12mm		>12mm	
	m	a	m	a	m	a	m	a	m	a
Hymenoptera										
mean	3.8	3.8	1.3	1.5	1.4	2.1	1.4	1.3	0.9	0.5
range	1-10	0-8	0-3	0-4	0-5	0-5	0-6	0-3	0-11	0-2
Diptera										
mean	13.1	10.8	3.6	1.6	1	0.5	0.1	0.2	0.4	
range	3-20	5-19	0-47	0-5	0-5	0-2	0-1	0-1	0-3	
Coleoptera										
mean	3.8	2.8	2.1	1.8	0.1	0.1				
range	3-5	1-6	0-7	0-7	0-1	0-1				
misc. orders										
mean	1.8	1.5	1	0.5	0.3		0.3	0.1	0.2	
range	0-3	0-5	0-3	0-2	0-2		0-1	0-1	0-1	

Table 5 continued

Harrington 1993 (8 daily aggregate samples)

	<3mm		3-6mm		6-9mm		9-12mm		>12mm	
	m	a	m	a	m	a	m	a	m	a
Hymenoptera										
mean	4	3.6	1.6	2.4	1.8	1.4	0.8	0.8		
range	1-7	1-5	0-4	0-5	0-4	0-2	0-1	0-1		
Diptera										
mean	5.5	5.4	3.1	2.3	0.5	0.4	0.1		0.1	0.1
range	1-10	0-9	0-8	0-6	0-1	0-2	0-1		0-1	
Coleoptera										
mean	2.8	1.6	1	0.5	0.4	0.3	0.1		0.1	
range	0-5	0-3	0-3	0-1	0-2	0-1	0-1		0-1	
misc. orders										
mean	1.4	0.8	0.5	0.4	0.1		0.1		0.1	
range	0-5	0-2	0-2	0-2	0-1		0-1		0-1	

Kenwood Wildlife Refuge 1992 (8 daily aggregate samples)

	<3mm		3-6mm		6-9mm		9-12mm		>12mm	
	m	a	m	a	m	a	m	a	m	a
Hymenoptera										
mean	15.9	20.4	0.3	1.9	0.2	0.7	0.9	1	0.1	
range	11-28	9-45	0-1	0-6	0-1	0-2	0-2	1	0.1	
Diptera										
mean	30.1	26	3.9	2.4		0.1		0.3		
range	19-36	15-48	1-8	0-6		0-1		0-1		
Coleoptera										
mean	6.4	6.6	2.1	1.9	0.4	0.3	0.3	0.4		
range	3-11	1-13	0-5	0-3	0-1	0-2	0-2	0-1		
misc. orders										
mean	4	3.8	1.8	1			0.1	0.1		
range	1-6	2-5	0-3	0-2			0-1	0-1		

Although the sample base from the additional plants is limited by the variation in flowering episodes data in Appendix 2 indicate that numerous taxa are shared between local assemblages of mass-flowering trees. This shared pool includes species (obligates) (e.g., within the families Buprestidae, Cantharidae, Mordellidae, Scarabaeidae, Tiphidae, Colletidae, Halictidae, Arctiidae) that possess mouthparts adapted to feeding from flowers, and taxa with no obligate morphological adaptation to feeding from flowers (e.g., Chrysomelidae, Coccinellidae, Dermestidae, Melyridae). Shared taxa also include Diptera from the families Calliphoridae, Lauxaniidae and Platystomatidae. These possess mouthparts adapted to feed from a variety of liquids.

Interestingly, *Trigona*, *Lasioglossum* (Halictidae), Megachilidae and Colletidae-Euryglossinae bees were not recorded from any of the plant species sampled at Harrington but occur elsewhere in the region (Williams and Adam 1997). The scarabaeid beetle genus *Phyllotocus*, which can occur prolifically on *Guioa semiglauca* (F. Muell.) Radlk. (Sapindaceae) at Harrington, and *Acmena smithii* (Poiret) Merr. & Perry and *Waterhousea floribunda* (F. Muell.) B. Hyland (Myrtaceae) elsewhere in the region, occurred only rarely at the Harrington site on *A. excelsa* (Williams 1995).

Butterflies and cetonine beetles were collected on *Alphitonia excelsa* flowers at Harrington but were not collected from other rainforest trees at the site. These included *Junonia villibe callibe*, *Hypolimna bolina nerina*, *Danaus hamata hamata* (Nymphalidae), *Delias nysa nysa* (Pieridae), *Candalides absimilis*, *Deudorix epijarbas diovis*, *Erysichton lineata lineata* (Lycaenidae), *Graphium eurypylus lycaon* (Papilionidae), *Polystigma punctatum* and *Eupoecila australasiae* (Scarabaeidae - Cetoniinae). These species are widely distributed in northern New South Wales and have been recorded elsewhere in the study area (Williams 1995, G. Williams and J. Brown unpublished data). Cetoniinae and butterflies undertake frequent interplant movements and are likely to make important contributions to out-crossing.

DISCUSSION

The slightly sticky pollen of *A. excelsa* is not easily displaced from the anthers, so it is unlikely that wind pollination occurs. The protandrous pattern of flower opening, and the recurving of petals which articulate the stamens away from the developing ovaries, may militate against self-fertilisation or interference with stigmatic function by self-pollen. Flower longevity is considerably longer than the average of less than two days recorded by Stratton (1989) for Costa Rican tree species, but is similar to the mean flower longevity of most subtropical trees investigated by Williams (1995).

There is no obvious adaptation of flowers to visits by specialised insects (e.g., long-tongued bees) and the shallow, readily accessible, perianth allows visitation by numerous insects, the majority of which are less than 6 mm in length. Pollination in *A. excelsa* appears to be a flexible general entomophilous system in which the contributions made by individual insect orders and lower rank taxa vary spatially and temporally. Primack (1978) considered that unspecialised floral syndromes may be an adaptation to highly variable pollinator assemblages. Unspecialised flower structures permit visits by a broad range of pollinators, and this flexibility in the use of available pollination vectors facilitates colonisation of new areas (Primack 1978). However, we know little about the cues, environmental or otherwise, that influence pollinator abundance and diversity at *A. excelsa* populations, and within and across different seasons.

Many of the insects visiting *A. excelsa* also visit flowers of other species. Successful pollination in plants utilising a pool of generalist pollinators is likely to be enhanced if competition between plant species for the same pool of insects is reduced. On the Mid-North coast of New South Wales most lowland rainforest tree species have ceased flowering by the beginning of summer, with the majority of species flowering

from October to December (Williams 1995, G. Williams unpubl. data). Flowering of *A. excelsa* populations is relatively synchronous and occurs after this spring-summer flowering peak. Populations flower for approximately 6-8 weeks. *Alphitonia excelsa* is the last widespread lowland rainforest tree in the region to flower in abundance during summer. This may increase the chances of pollination but also substantially extends the availability of floral resources to nectar and pollen-dependent species (and species preying on them). *Alphitonia excelsa*, over three seasons at Harrington, provided the greatest number of species collected during our broader study of lowland subtropical rainforest (Williams 1995), and the late season flowering, when few other flowers are available, may explain this abundance.

The majority of insect visitors to *A. excelsa* are mainly Diptera and Hymenoptera but whether these are efficient as pollinators is not known. Williams and Adam (1998) document pollen loads from large-sized Coleoptera, Diptera and Hymenoptera visiting *A. excelsa* indicating the potential, of at least a subset, of insect visitors to transport pollen.

Orders, families and genera varied in daily, seasonal and geographic abundance and diversity on *A. excelsa* flowers and there were marked differences between the composition of faunas visiting *A. excelsa* populations at Harrington and Kenwood Wildlife Refuge. Hingston and Potts (1998) record geographic variation in insect assemblages visiting flowering *Eucalyptus globulus* populations in Tasmania. Although there is temporal heterogeneity in occurrence of insects at *A. excelsa* blossoms, there is a general peak in abundance of anthophilous taxa and individuals approximately 2-4 weeks after the onset of flowering.

Although *A. excelsa* has not been previously studied, Irvine and Armstrong (1988) discuss pollination of the related *A. petriei* in tropical Queensland. This species is also a pioneer, mass-flowering, bisexual protandrous rainforest tree. Unlike *A. excelsa*, *A. petriei* flowers from September to November (Irvine and Armstrong 1990), during the tropical dry season. Irvine and Armstrong (1988) found that *A. petriei* has a flexible entomophilous pollination system (similar to that suggested by the floral visitors to *A. excelsa*) dominated by Diptera and Coleoptera, and to a lesser degree wasps. *Apis mellifera* was also an active visitor to *A. petriei* flowers.

Irvine and Armstrong (1988) recorded ten Coleoptera species from limited observations on *A. petriei*, and stated "In terms of cantharophily [beetle pollination syndrome], it is the specialised inflorescence type, attracting predominantly medium-sized, non-flower-damaging, nectar/pollen-feeding beetles...". Although we collected 28 beetle families on *A. excelsa*, only Buprestidae, Cantharidae, Elateridae, Lycidae, Mordellidae, Rhipiphoridae and Scarabaeidae included taxa that are considered specialised blossom visitors. Representatives from these families were generally uncommon, and did not approach the diversity of Coleoptera encountered on mass-flowering Myrtaceae elsewhere in the study region (Williams 1995). Coleoptera are numerous on a number of mass-flowering tree species in late spring and early summer in the region (Williams 1995).

In addition to *A. petriei*, tropical Australian rainforest pollinator faunas, dominated generally by combinations of Diptera, Hymenoptera and Coleoptera, are documented from *Flindersia brayleyana* F. Muell. (Flindersiaceae) (Irvine and Armstrong 1988, 1990), *Neolitsea dealbata* (R. Br.) Merr., *Litsea leefeana* (F. Muell.) Merr. (Lauraceae), and *Diospyros pentamera* (Wools and F. Muell.) F. Muell. (Ebenaceae) (House 1985, 1989). House (1989) found that Diptera were the most abundant visitors to flowers of dioecious *N. dealbata*, *L. leefeana* and *D. pentamera*, but that Coleoptera were the most important in carrying pollen to pistillate *D. pentamera* trees. Generalist insect pollination systems are widely recorded from a number of plant communities (e.g., Bawa 1990, Herrera 1988, Moldenke 1975, Petanidou and Ellis 1993, Primack 1978) and have also been recorded from individual plant species (e.g., Ervik and Feil 1997, Kato 2000.). However, rainforest invertebrate assemblages dominated by Diptera, Hymenoptera and Coleoptera are not

restricted to anthophilous insects. For example, Basset and Kitching (1991) collected approximately 42,000 arboreal arthropods (which are likely to have included a proportion of anthophilous taxa) in tropical Queensland rainforest using composite 'malaise-window' intercept traps designed to minimize taxonomic bias in the fauna being sampled; 27% of individuals were Coleoptera, 41% were Diptera and 11.3% were Hymenoptera.

The putative flexible pollination system of *A. excelsa* would permit it to colonise rainforest margins and regenerating, previously cleared, landscapes without reliance on specialised pollination mutualists. An ability to draw upon a wide taxonomic range of polylectic pollinators, and a lack of dependence on any one taxon, or subset of pollinator taxa, make such species suitable for 'nurse crop' plantings in the restoration of rainforest remnants and corridors (although species used in rehabilitation plantings should naturally occur in the landscape subject to restoration). The late season flowering of *A. excelsa* provides an extension of floral resources to flower-dependent faunas surviving in small lowland rainforest remnants. This late season availability of resources may be important to the conservation of relict insect populations surviving in forest fragments where individual tree species may maintain small populations, and where floral resources are likely to be spatially and temporally limited.

ACKNOWLEDGEMENTS

We thank Drs David McAlpine, Shane McEvey, Daniel Bickel, Courtenay Smithers (Australian Museum, Sydney), Ken Walker (Museum of Victoria, Abbotsford), Terry Houston (Western Australian Museum, Perth), Graham Brown (Museum and Art Gallery of the Northern Territory, Darwin), and John Lawrence, Elwood Zimmerman, Ian Naumann, Laurence Mound and Don Colless (C.S.I.R.O., Canberra) for identifying a number of the insects. Dr Caroline Gross (University of New England, Armidale) is thanked for suggestions and comments on an earlier version of this paper. Thusnelda Lehner kindly helped with fieldwork.

REFERENCES

- Baker, H.G. (1955). Self-compatibility and establishment after 'long-distance' dispersal. *Evolution* 9, 347-348.
- Basset, Y. and Kitching, R.L. (1991). Species number, species abundance and body length of arboreal arthropods associated with an Australian rainforest tree. *Ecological Entomology* 16, 391-402.
- Bawa, K.S. (1990). Plant-pollinator interactions in tropical forests. *Annual Reviews in Ecology and Systematics* 21, 399-402.
- Dafni, A., Lehrer, M. and Kevan, P.G. (1997). Spatial flower parameters and insect spatial vision. *Biological Reviews* 72, 239-282.
- Ervik, F. and Feil, J.P. (1997). Reproductive biology of the monoecious understorey palm *Prestoea schultzeana* in Amazonian Ecuador. *Biotropica* 29, 309-317.
- Gross, C.L. (1993). The breeding system and pollinators of *Melastoma affine* (Melastomataceae); a pioneer shrub in tropical Australia. *Biotropica* 25, 468-474.
- Harden, G.J. (ed.) (1990). *Flora of New South Wales*. Volume 1. (New South Wales University Press, Kensington).
- Harrington, G.N., Irvine, A.K., Crome, F.H.J. and Moore, L.A. (1997). Regeneration of large-seeded trees in Australian rainforest fragments: a study of higher order interactions. In *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. (Eds. W.F. Laurance and R.O. Bierregaard). (The University of Chicago Press, Chicago).
- Herrera, J. (1988). Pollination relationships in Southern Spanish Mediterranean shrublands. *Journal of Ecology* 76, 274-287.
- Hingston, A.B. and Potts, B.M. (1998). Floral visitors of *Eucalyptus globulus* subsp. *globulus* in eastern Tasmania. *Tasforests* 10, 125-173.
- House, S.M. (1985). *Relationships between breeding and spatial pattern in some dioecious tropical rainforest trees*. Ph.D. thesis. Australian National University, Canberra.
- House, S.M. (1989). Pollen movement to flowering canopies of pistillate individuals of three rainforest trees in tropical Australia. *Australian Journal of Ecology* 14, 77-94.
- Ireland, J.C. and Griffin, A.R. (1984). Observations on the pollination ecology of *Eucalyptus muelleriana* Howitt in East Gippsland. *The Victorian Naturalist* 101, 207-211.

- Irvine, A.K. and Armstrong, J. (1988). Beetle pollination in Australian tropical rainforests. *Proceedings of the Ecological Society of Australia* **15**, 107-113.
- Irvine, A.K. and Armstrong, J. E. (1990). Beetle pollination in tropical forests of Australia. In *Reproductive ecology of tropical forest plants*. Volume 7. (Eds. K.S. Bawa and M. Hadley). (Unesco, Parthenon, Carnforth).
- Kato, M. (2000). Anthophilous insect community and plant-pollinator interactions on Anami Islands in the Ryukyu Archipelago, Japan. *Contributions from the Biological Laboratory, Kyoto University* **29**, 157-252.
- Kitching, R.L., Orr, A.G., Thalib, L., Mitchell, H., Hopkins, M.S. and Graham, A.W. (2000). Moth assemblages as indicators of environmental quality in remnants of upland Australian rainforest. *Journal of Applied Ecology* **37**, 284-297.
- Kurahashi, H. (1989). Family Calliphoridae. Chapter 109. In *Catalog of the Diptera of the Australasian and Oceanian Regions* (Ed N.L. Evenhuis). (Bishop Museum Press, Honolulu, and E.J. Brill, Leiden).
- Laurance, W.F. (1997). Hyper-disturbed parks: edge effects and the ecology of isolated rainforest reserves in tropical Australia. In *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. (Eds. W.F. Laurance and R.O. Bierregaard). (The University of Chicago Press, Chicago).
- Moldenke, A.R. (1975). Niche specialisation and species diversity along an altitudinal transect in California. *Oecologica (Berl.)* **21**, 219-242.
- Petanidou, T. and Ellis, W. (1993). Pollinating fauna of a phryganic ecosystem: composition and diversity. *Biodiversity Letters* **1**, 9-23.
- Primack, R.B. (1978). Variability in New Zealand montane and alpine pollinator assemblages. *New Zealand Journal of Ecology* **1**, 66-73.
- Stratton, D.A. (1989). Longevity of individual flowers in a Costa Rican cloud forest: ecological correlates and phylogenetic constraints. *Biotropica* **21**, 308-318.
- Thompson, F.C. and Vockeroth, J.R. (1989). Family Syrphidae. Chapter 51. In *Catalog of the Diptera of the Australasian and Oceanian Regions* (Ed N.L. Evenhuis). (Bishop Museum Press, Honolulu, and E.J. Brill, Leiden).
- Williams, G.A. (1993). *Hidden rainforests: subtropical rainforests and their invertebrate biodiversity*. (New South Wales University Press, Kensington).
- Williams, G.A. (1995). *Pollination ecology of lowland subtropical rainforests in New South Wales*. Ph.D. thesis. University of New South Wales, Kensington.
- Williams, G.A. and Adam, P. (1994). A review of rainforest pollination and plant-pollinator interactions with particular reference to Australian subtropical rainforests. *The Australian Zoologist* **29**, 177-212.
- Williams, G.A. and Adam, P. (1995). Records of aculeate wasps from flowering subtropical rainforest trees. *The Australian Entomologist* **22**, 51-58.
- Williams, G.A. and Adam, P. (1997). The composition of the bee (Apoidea: Hymenoptera) fauna visiting flowering trees in New South Wales lowland subtropical rainforest remnants. *Proceedings of the Linnean Society of New South Wales* **118**, 69-95.
- Williams, G.A. and Adam, P. (1998). Pollen loads collected from large insects in Australian subtropical rainforests. *Proceedings of the Linnean Society of New South Wales* **120**, 49-67.

APPENDIX 1

List of insect families and genera collected from

A. excelsa at Harrington (1990-93) and Kenwood Wildlife Refuge (1991-92) (genera not determined for all families) (numbers in columns indicate number of species recorded in individual seasons).

Families	Genera	Harr 90-91	Harr 91-92	Harr 92-93	Ken 91-92
BLATTODEA					
Blattellidae	<i>Ectoneura</i>	1			
COLEOPTERA					
Anobiidae		1			
Anthicidae	<i>Anthicus</i>	1	1	1	1
	? <i>Anthicus</i>				1
Attelabidae	<i>Auletobius</i>		1		1
Buprestidae	<i>Castiarina</i>	2	2		2
	<i>Cisseis</i>	1			
	<i>Melobasis</i>	1			
	<i>Neocuris</i>	1			
	<i>Torresita</i>			1	
Cantharidae	<i>Chauliognathus</i>		1	1	1
Carabidae	<i>Sarcothrocrepis</i>		2		
Cerambycidae	<i>Tillomorpha</i>		1	1	

Chrysomelidae	<i>Cryptocephalus</i>		1		
	<i>Ditropidus</i>	1		1	2
	? <i>Ditropidus</i>				1
	<i>Monolepta</i>	1	>/=4	1	5
Cleridae	<i>Lemidia</i>				1
Coccinellidae	<i>Amidellus</i>	1	1	1	1
	<i>Cryptolaemus</i>	1	1		
	<i>Egleis</i>				1
	<i>Epilachna</i>	1			
	<i>Orchus</i>				1
	<i>Rhizobius</i>		2	1	
	? <i>Rhizobius</i>	2		1	
	<i>Rodolia</i>	1		1	
Corylophidae	<i>Sericoderus</i>	1	1	1	1
Curculionidae	<i>Balanerhinus</i>		1		
	<i>Baris</i>				1
	<i>Cyrtalia</i>				1
	<i>Meriphys</i>				1
	<i>Neolaemaraccus</i>	1			
Dermestidae	<i>Anthrenocerus</i>			1	>1
	? <i>Anthrenocerus</i>	1	1		1
	<i>Thaumaglossa</i>	1	1		
Elateridae	<i>Megapenthes</i>				1
	<i>Ophidius</i>			1	
Euglenidae	<i>Aderus</i>				2
	? <i>Aderus</i>			1	1
Hydrophilidae	<i>Pseudohydrobius</i>		1		
Lathridiidae	<i>Corticara</i>		1		1
Lycidae	<i>Porrostoma</i>				2
	? <i>Porrostoma</i>				1
Melyridae	<i>Carphurus</i>		1	1	1
	? <i>Carphurus</i>				1
	<i>Dicranolaius</i>	1	1	1	
	<i>Helcogaster</i>				>2
	? <i>Helcogaster</i>				1
	<i>Neocarphurus</i>		1		
Mordellidae	<i>Hoshihananomia</i>	1	1		
	<i>Mordella</i>		>1	>1	>2
	<i>Mordellistena</i>				1
	? <i>Mordellistena</i>		1		
	<i>Tomoxia</i>	1			
	? <i>Tomoxia</i>	1	1		
Nitidulidae	<i>Eपुरaea</i>		1		
Phalacridae	<i>Litochrus</i>	1	>1	>1	
	? <i>Litochrus</i>	1	1		>1
	<i>Parasemus</i>			1	1
	? <i>Phalacrus</i>	1			1
	<i>Paromarteon</i>				1
Pythidae	<i>Macrosiagon</i>	1	1		
Rhipiphoridae	<i>Cheiragra</i>		1		
Scarabaeidae	<i>Eupoecila</i>	1	1		
	<i>Glycyphana</i>				1
	<i>Heteronyx</i>		1		
	<i>Phyllotocus</i>		1		
	<i>Polystigma</i>	1			1
Scirtidae	<i>Pseudomicrocara</i>		2		
	? <i>Pseudomicrocara</i>		1		
	<i>Scirtes</i>		2		
	? <i>Scirtes</i>				1
Staphylinidae	genus near <i>Anotylus</i>				1
Tenebrionidae	? <i>Apellatus</i>			1	
	<i>Ecnolagria</i>				1
	<i>Nocar</i>		1		
	<i>Ommatophorus</i>	1			

COLLEMBOLA				
Entomobryidae	<i>?Lepidosira</i>	1		
DIPTERA				
Bibionidae	<i>Biblio</i>	1	1	
Bombyliidae	<i>Geron</i>	1		1
	<i>Ligyra</i>		1	
	<i>Pseudopenthes</i>		1	
Calliphoridae	<i>Chrysomya</i>		1	
	<i>Paramenia</i>	1	1	
	<i>Stomorphina</i>	>1	>1	>1
Cecidomyiidae			1	1
Ceratopogonidae				1
Chironomidae				2
Chloropidae				1
	<i>Apotropina</i>		1	
Culcidae		2		
Dolichopodidae	<i>Krakatauia</i>	1	1	
Drosophilidae	<i>Drosophila</i>		1	1
	<i>Leucophenga</i>		1	
	<i>Nesiodrosophila</i>			1
Empididae			1	
Ephidridae		1		
Lauxaniidae	<i>Homoneura</i>		1	
	<i>Melanina</i>			1
	<i>?Melanina</i>		1	
	<i>Sapromyza</i>	1	1	
	<i>Steganopsis</i>	1		
	<i>Trypetisoma</i>	1		
Milichidae				1
Muscidae	<i>Musca</i>	1	1	
Mycetophilidae			1	>1
Nemestrinidae	<i>Cyclopsidea</i>	1		
Phoridae			1	1
Platystomatidae	<i>Duomyia</i>	1	2	
	<i>Euprosopia</i>		1	
	<i>Microepicausta</i>	1		1
	<i>Pogonortalis</i>	1	1	1
	<i>Rivellia</i>	1	2	2
Psychodidae			2	
Rhagionidae	<i>Chrysopilus</i>			1
Sarcophagidae	<i>Sarcorohdendorfia</i>	2	1	1
Scatopsidae				1
Sepsidae	<i>Australosepsis</i>		1	
	<i>?Lasionemapoda</i>			1
	<i>?Parapalaeosepsis</i>	1		
	<i>Sepsis</i>	1	2	2
Stratiomyidae	<i>Acanthasargus</i>			1
	<i>Damaromyia</i>			1
	<i>Hermetia</i>		1	
	<i>Odontomyia</i>		4	1
Syrphidae	<i>Dideopsis</i>	1	1	
	<i>Eristalinus</i>	2		1
	<i>Mesembrios</i>	1	1	
	<i>?Xanthogramma</i>			1
Tabanidae				1
	<i>Scaptia</i>		1	
	<i>?Tabanus</i>		2	
Tachinidae	<i>Austrophorocera</i>	1		
	<i>Blepharella</i>		1	1
	<i>?Blepharella</i>		1	
	<i>Blepharipa</i>	1		
	<i>Prosenia</i>	1		
	<i>Rutilia</i>	1	1	

